NeoBiota 81: 157–182 (2023)
doi: 10.3897/neobiota.81.89450
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Effects of the invasive leafy spurge (*Euphorbia esula* L.) on plant community structure are altered by management history

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Academic editor: E. Wandrag | Received 24 June 2022 | Accepted 4 January 2023 | Published 27 January 2023

Citation: Liu C, Groff T, Anderson E, Brown C, Cahill Jr JF, Paulow L, Bennett JA (2023) Effects of the invasive leafy spurge (*Euphorbia esula* L.) on plant community structure are altered by management history. NeoBiota 81: 157–182. https://doi.org/10.3897/neobiota.81.89450

Abstract

Invasive species threaten biodiversity and ecosystem functioning, often causing changes in plant community composition and, thus, the functional traits of that community. Quantifying changes in traits can help us understand invasive species impacts on communities; however, both the invader and the plant community may be responding to the same environmental drivers. In North America, leafy spurge (*Euphorbia esula* L.) is a problematic invader that reduces plant diversity and forage production for livestock. Its documented effects on plant communities differ amongst studies, however, potentially due to differences in productivity or land management. To identify the potential effects of leafy spurge on plant communities, we quantified leafy spurge abundance, plant species richness, forage production, functional group composition and community weighted mean traits, intensively at a single site and extensively across ten sites differing in management. We then tested how leafy spurge abundance related to these variables as a function of site management activities. Leafy spurge abundance was consistently associated with fewer plant species, reduced forage production and more invasive grass. Community-weighted specific root length also consistently increased with leafy spurge abundance, suggesting that belowground competition may be important in determining co-existence with leafy spurge. Other changes were dependent on management. Native forbs were excluded as leafy spurge became more abundant, but only in grazed sites as these species were already absent from ungrazed sites. Taller plants better persisted in dense leafy spurge patches, but only in grazed sites, consistent with either facilitation of taller species via associational

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defences or competitive exclusion of shorter species in ungrazed sites and dense leafy spurge patches. These results show that, despite some emergent properties of invasion, management context can alter invasion impacts by causing changes in the plant community and its interactions with the invader.

Keywords
co-existence, competitive exclusion, ecosystem function, exotic species, functional traits, invasion impacts, overgrazing, passenger-driver, plant height, specific root length

Introduction

Invasive plants can have strong effects on the structure and function of plant communities. When abundant, invasive plants exclude or suppress many plant species, which can reduce the diversity and functioning of resident plant communities (Levine et al. 2003; Vilà et al. 2011). In addition to driving changes in plant communities and ecosystems, invasive species can also be passengers of such change, increasing in abundance as a consequence of past land-use or management and any consequent ecosystem degradation (DiTomaso 2000; MacDougall and Turkington 2005; Carboni et al. 2016; Riibak et al. 2020). Isolating the effects of invasive plants on community structure and function is, therefore, challenging as it is unclear whether the invaders are driving or responding to community and ecosystem changes (White et al. 2012). By studying how invasive plant abundance is associated with changes in the plant community across environments and different management histories, we can potentially unravel some of these complexities, especially if we consider changes in the functional composition of the community.

Changes in the average functional traits of the species in the community, weighted by their relative abundance (the community weighted trait means), can be used to infer the ecological processes affecting community assembly as environmental and biotic filters select for specific traits (Laughlin 2014; Kraft et al. 2015; Bennett et al. 2016). Quantifying trait changes along gradients of invader abundances can also help understand invader impacts (Sodhi et al. 2019). Inferences on invader impacts may be obscured, however, if comparing amongst systems differing in their management (e.g. grazed or not) or ecology (e.g. differences in resource limitation) (White et al. 2012). For example, in productive ecosystems, increases in the average height of the remaining plant species in dense invader patches suggests that shade-intolerant shorter species were excluded due to competition for light (Hejda et al. 2019). Increases in plant height with invader abundance may not be possible in less productive systems if resource limitation limits the establishment of tall species (Daou et al. 2021) or when herbivory rates on taller species are high (Diaz et al. 2007), especially if the invader is not consumed and herbivory pressure remains constant (enemy release; Gross et al. (2015)).

In this study, we explore the effects of invasive species on plant community structure and ecosystem function focusing on leafy spurge (*Euphorbia esula* L.), a problematic invader throughout much of the North American Great Plains (Bradley et

al. 2009). Leafy spurge is an aggressively clonal plant with a deep root system from which it can generate new shoots (Best et al. 1980). Leafy spurge is also unpalatable to cattle (Hein and Miller 1992) which reduces forage production for livestock and, thus, ecosystem function, in grazing systems and makes it an economically important invasive species (Leistritz et al. 2004). When combined with its deep root system, low palatability may allow leafy spurge to flourish in systems like the Great Plains where water is often limiting and livestock grazing pressure is often intense (Epstein et al. 1997). Additionally, leafy spurge benefits more from mycorrhizal fungi, which provide plants with nutrients and other benefits in exchange for carbon, than most species in the Great Plains (Reinhart et al. 2017) and may increase the abundance and diversity of mycorrhizal fungi (Lekberg et al. 2013) to its advantage. Consequently, leafy spurge can form dense patches with reduced plant species richness, reduced forage production and significant alterations to other ecosystem functions (Belcher and Wilson 1989; Butler and Cogan 2004; Larson and Larson 2010; Gibbons et al. 2017).

Despite being associated with declines in plant diversity, leafy spurge effects on the composition and function of invaded communities are unclear. Results are often inconsistent at the functional group level, with some studies finding leafy spurge to be associated with a loss of native grasses and others showing a negative association between leafy spurge and native forbs (Belcher and Wilson 1989; Larson and Larson 2010). Inconsistency in results amongst studies may be due to differences in past management, especially if leafy spurge is not driving changes in community structure, but simply invading already degraded ecosystems (i.e. it is a passenger; MacDougall and Turkington (2005)). Overgrazing at some sites could facilitate leafy spurge invasion by reducing grass abundances, resulting in negative relationships between leafy spurge and native grasses (DiTomaso 2000; Li et al. 2017). Leafy spurge is also positively associated with invasive grasses (Belcher and Wilson 1989) that can increase with overgrazing (DiTomaso 2000) and cause loss of native grasses and forbs (Bennett et al. 2014), potentially obscuring any leafy spurge effects on the plant community. Historical control of high-density leafy spurge invasions with herbicides or small ruminant grazing can also reduce the abundance of non-target forbs, which could result in a negative association between leafy spurge and forb abundances if leafy spurge recovers more rapidly than the native forbs (Thilmony and Lym 2017). Accounting for land management activities when assessing the effect of leafy spurge on the resident community is thus important.

Quantifying the relationship between leafy spurge abundance and community-weighted trait means may also help us develop hypotheses about how leafy spurge affects the plant community and associated ecosystem functions (Castro-Díez et al. 2016). Given the ecology of leafy spurge and grassland ecosystems, we focus on traits related to competition, grazing response and mycorrrhizas. Changes in the community mean traits towards more resource acquisitive and competitive values could suggest that only competitive species can co-exist with leafy spurge or that leafy spurge does better in high resource environments. Changes in these traits towards those associated with stress tolerance and grazing avoidance could suggest that either species that tolerate increased grazing pressure can co-exist with leafy spurge or that leafy spurge tends

to invade stressful environments. Alternatively, an increase in community root thickness and tissue density could suggest that stress tolerant species or those that exploit mycorrhizal fungi best co-exist with leafy spurge or that leafy spurge is more likely to invade areas where these plants are found. We include height, leaf area and specific leaf area (SLA) as taller plants with larger leaves that are produced with less tissue investment can improve competition for light (Pérez-Harguindeguy et al. 2013; Bennett et al. 2016). Similarly, we include root diameter and specific root length (SRL) as narrower roots that require less investment in tissue can increase foraging ability and competition for soil resources (Freschet et al. 2015; Bennett et al. 2016; Bergmann et al. 2020). Some of these traits (height and SLA) are also associated with herbivory avoidance and shorter plants with tougher leaves may indicate stronger effects of grazing pressure (Diaz et al. 2007), whereas others (low SRL and high root diameter) can be associated with reliance on mycorrhizal fungi (Bergmann et al. 2020). By comparing these relationships amongst environmentally diverse sites that differ in their management and, thus, differ in their expected traits, we can determine whether leafy spurge is consistently associated with specific changes in the trait composition of the community and use those changes to develop hypotheses about the mechanisms by which leafy spurge may cause community change.

To explore the association amongst leafy spurge abundance, species richness, the trait composition of the resident community and forage production for livestock producers, we use two different surveys: one in which a single heavily invaded 9,300 ha site was intensively sampled and a broader survey that covered 10 different sites across 600 km. Sites in the multi-site survey differed in their usage (cattle grazing versus recreational) and weed management protocols (herbicide versus non-herbicide), allowing us to infer whether land management affects the association between leafy spurge and the plant community. In each survey, we collected plant composition and abundance data to test whether leafy spurge was negatively associated with species richness and forage production (measured as graminoid abundances and nutrient content) as estimates of ecosystem function relevant to local land managers. We also test for leafy spurge abundance associations with functional group composition and community-weighted trait means. We use these analyses to infer leafy spurge effects on plant community structure and how the observed relationships may be altered by land management.

Methods

Intensive survey

The intensive survey was conducted at the Elbow community pasture (51.0°N, -106.3°W), a 9,300-ha former government pasture now managed by a local cattle producer group. The Elbow site was selected due to its large leafy spurge invasion across a broad area. Leafy spurge has been managed at Elbow since 1991 through small ruminant (sheep and goats) grazing, complemented by the release of biocontrol agents

(*Aphthona* spp.) in some areas and herbicide application along trails and boundaries. All areas of the pasture are lightly grazed by cattle, but not all areas are grazed by small ruminants due to heterogeneity in leafy spurge and difficulties managing small ruminants in wooded areas. Vegetation is typical of sandy soils in the mixed grass ecoregion of Saskatchewan (Thorpe 2014), but there are areas with high tree and shrub cover and others that were aerially seeded to *Agropyron cristatum* approximately 40 years ago, but since managed extensively. To focus on leafy spurge invasion in grasslands, areas dominated by woody plants were avoided. Areas with *Agropyron cristatum* were included, although a lack of data on where seeding occurred meant that we could not separate seeded from unseeded transects. Areas where herbicide was used were avoided, but transects included areas grazed by small ruminants (24 transects) and those not grazed by small ruminants (six transects).

In 2018, we identified 18 stratified random sampling locations to maximise spatial spread across the site. We identified each grassy area of the pasture using georeferenced aerial photos and selected one to three locations within each area haphazardly, with the number of locations dependent on grassy patch size. We then travelled to these locations and identified the nearest leafy spurge patch to use for our survey. We also sampled four locations that were used historically for monitoring the site (22 total locations in 2018). In 2019, we returned to these sampling locations and added eight new locations using the same protocols as above (30 total locations in 2019). At each sampling location, we established two perpendicular 20 m transects that intersected at the centre of the leafy spurge patch. To quantify the plant community in both years, we estimated percent cover in a 0.25 m^2 quadrat at the transect intersections and at 5 m intervals in each cardinal direction (nine quadrats per transect). Of these quadrats, four were excluded from these analyses as they were placed within grazing cages and, thus, differed in grazing history. As a result, we used 194 quadrats in 2018 and 266 quadrats in 2019. We used these same quadrats to measure leafy spurge stem density as an additional estimate of leafy spurge abundance. In 2019, we clipped four additional 0.1 m^2 quadrats to 2 cm stubble height to collect plant biomass, with quadrats placed 2 m from the centre of the transect in each direction. These samples were sorted into litter, graminoids, forbs, shrubs and leafy spurge, before drying them at 60 °C for 72 h and weighing. We then calculated herbaceous biomass as the sum of graminoid, forb and spurge biomass, which served as an estimate of site productivity to include as a covariate in our models. As these lands are primarily managed for livestock, forage production is the primary ecosystem function of concern to land managers. We, therefore, estimated forage production as graminoid biomass and, to assess forage quality, we ground the graminoid samples and measured nitrogen content using a LECO 628 elemental analyser (LECO Corporation, St. Joseph, Missouri, USA).

Multi-site survey

For the multi-site study, we selected three regions in addition to Elbow where leafy spurge invasion is common. These areas cover approximately 600 km from NW to SE

along the northern boundary of the Great Plains and were centred on the following locations: west (52.7°N, -109.1°W); central (52.0°N, -106.8°W); and south (49.3°N, -104.0°W). In each region, we visited sites where leafy spurge invasion had been reported to municipal and provincial governments. Sites were selected if we were able to find a leafy spurge patch of at least 25 m^2 where leafy spurge did not exhibit signs of recent herbicide application. These patches were designated as blocks for inclusion in a separate experiment and, for grazed sites only, were fenced to exclude growing season grazing for the duration of the study. At some sites, we created multiple blocks if we found multiple physically distinct (non-contiguous) patches that were at least 10 m apart. Experimental plots were not used in the current analyses. In total, we created five blocks in the Elbow region, 10 in the central region, five in the west and five in the south. Three blocks were intensively disturbed over the course of the study (see Suppl. material 1: table S1) so were excluded from our analyses. Blocks from the Elbow region were at least 200 m from any transects in the intensive survey conducted at that site. All sites were classified as mixed grass prairie historically, although many were now dominated by invasive grasses (primarily *Bromus inermis*, *Poa pratensis* or *Agropyron cristatum*). Soils were variable amongst blocks, although most would be characterised as sandy dark brown or black chernozems (Suppl. material 1: table S1).

Past management and usage were variable across the sites. For management, we grouped sites into two categories: herbicide and other. We focus on herbicide application as broadleaf specific herbicides were commonly used (11 blocks) and have strong effects on community structure. Sites in the other category included sites with unknown management, but without any evidence of herbicide application (seven blocks), targeted small ruminant grazing (five blocks) and mowing (two blocks). For usage, we grouped sites into two categories: cattle grazing (18 blocks) and recreation (seven blocks). Past grazing intensity was unknown and, therefore, not accounted for.

As with the intensive survey, we estimated percent cover of all vascular plant species in 0.25 m^2 quadrats in late June and early July of 2018 and 2019. We collected six percent cover estimates per block in 2018 (144 quadrats), but this was reduced to 3–5 plots per block in 2019 due to time constraints (88 quadrats). All quadrats were placed within the fenced area for grazed sites or within 2 m of an experimental plot for ungrazed sites. Quadrat locations were selected to represent uninvaded areas and high leafy spurge densities within the block, although uninvaded areas were not always available, so we selected lowest density areas in those cases.

In both years, we clipped plant biomass in one 0.1 m^2 quadrat per block to obtain estimates of productivity as in the single site survey. Following weighing, we ground the graminoid biomass for nutrient analysis to explore changes in forage for cattle. We measured nitrogen as in the intensive survey in 2018, but measured nitrogen and phosphorus in 2019 as we were interested in phosphorus concentrations for the associated experiment. Nitrogen and phosphorus were analysed using an AA1 Autoanalyser (Seal Analytical Inc., Mequon, Wisconsin, USA) following Kjeldahl sulphuric acid digestion. Given that soil properties can have strong effects on the composition and traits of the plant community (Conradi and Kollmann 2016), we also collected ten soil samples

(2 cm wide and 15 cm deep) from within each block in 2019. These samples were pooled at the block level and homogenised prior to analysis. We analysed a subsample for texture using the hydrometer method (Bouyoucos 1962). Additional subsamples were ground and analysed for total carbon using a LECO C632 Soil Carbon Analyser (LECO Corporation, St. Joseph, Missouri, USA) and total nitrogen and phosphorus using the same procedure as for leaf tissues.

Trait measurements

For our trait analyses, we focus on five traits – average height, average leaf area, SLA, average root diameter and SRL – due to their associations with resource acquisition and tolerance strategies. For some species, plant traits were measured at the study sites, whereas trait data for others were taken from similar sites in Saskatchewan (Letts et al. 2015) or the neighbouring Province of Alberta (Kembel and Cahill 2011; Cahill 2020). Given that only two of the data sources measured the average height, we also included height data taken from the Flora of Alberta (Moss and Packer 1994). No single trait source included all species in the current study (see Suppl. material 1: table S2), so we used the average values across the data sources. We took the average across individuals, irrespective of source; however, we excluded all outliers, defined here as values greater or less than three times the standard deviation from the mean based on log transformed traits.

For traits measured in situ, we used standard protocols (Pérez-Harguindeguy et al. 2013) and focused on the most common species. We selected up to five individuals per species for analysis, although the number of plants measured was lower for less common species. Height was measured as the maximum vegetative height in situ for each plant. For height data taken from the flora, we used the average of minimum and maximum heights as an estimate of the average height for that species. Leaf area was measured as the average area of three mature leaves per plant using a Li-3000C leaf area meter (LI-Cor, Lincoln, Nebraska). All leaves were placed in sealed plastic bags with moist paper upon collection to prevent dehydration and shrinkage until they could be analysed. These leaves were then dried at 60 °C for 72 h and weighed to determine SLA. We also excavated each individual and collected a haphazard sample of their fine roots, which were stored in 70% ethanol solution until processing. Root samples were carefully washed over a 1-mm sieve then scanned at 400 dpi using an Epson Perfection V800 Photo scanner. Root diameter and root length were calculated using WinRHIZO Pro 2013a (Regent Instruments Inc.). The root samples were then dried at 60°C for 72 h and weighed to calculate SRL.

Functional groups and community weighted trait means

Using the quadrat level cover data, we calculated species richness as the number of vascular plant species. We then classified species into five groups: native forbs, native grasses, native shrubs, exotic forbs and exotic grasses. There were no exotic shrubs. We then calculated the proportion of species and total cover belonging to each functional

group. Using the percent cover data and the trait data described earlier, we also calculated the community weighted mean for each of the five focal traits using the R package FD (Laliberté and Legendre 2010). Leafy spurge was excluded from these calculations to avoid biasing the results. If we had included leafy spurge, the results would simply converge on the functional group or trait values of leafy spurge as it increased in abundance. To avoid results that were not actually representative of the community, we also excluded quadrats from the trait-based analyses if the available trait data represented less than 75% of the non-leafy spurge cover in that quadrat, resulting in the exclusion of 18/233 quadrats for the multi-site survey and 142/460 quadrats for the intensive single site survey.

Data analysis

To better understand how changes in functional group composition relate to changes in community weighted trait means, we ran five ANOVAs testing how each of the five traits (height, leaf area, SLA, root diameter and SRL) differed amongst the plant functional groups. Traits were the response variables and plant functional group was the fixed effect. Leaf area, SLA and SRL were log transformed to normalise the residuals.

For the remainder of our data analyses, we focused on testing the relationship between leafy spurge abundance and the following aspects of the plant community: 1) species richness, 2) graminoid forage production and nutrient content, 3) proportional abundance and richness of different functional groups and 4) community weighted means of the five traits. In these models, we also included multiple covariates to account for environmental influences on the leafy spurge-plant community relationships, so we ran additional analyses to see whether leafy spurge abundance also covaried with these variables. In all cases, the intensive single site survey and the multi-site survey were analysed separately. All data were analysed at the quadrat level, except for forage production, which was analysed at the transect or block level depending on the survey.

For the single-site survey, we analysed leafy spurge associations with species richness, the relative richness and abundance of the different functional groups and each of the community weighted trait means using separate mixed models in the lme4 package (Bates et al. 2015) in R v.4.1.2 (R Core Team 2021). In each model, we included leafy spurge abundance as either percent cover or stem density as the primary predictor. We decided which of the two predictors to use, based on the model having the lower Akaike's Information Criterion (AIC) score (Suppl. material 1: table S3). Additionally, we tested for non-linearity in the relationship by selecting the model with the lowest AIC score when leafy spurge abundance was included as a linear or quadratic predictor. We included an interaction between leafy spurge abundance and small ruminant grazing, but removed it if it increased AIC scores. Herbaceous plant biomass was also included as a covariate to represent variation in productivity amongst transects at the site and was square-root transformed to reduce the influence of outliers. Transect identity and year were included as random variables to account for the spatially and temporally repeated sampling. To test whether leafy spurge abundance covaried with the other predictors, we ran two additional mixed models with either leafy spurge cover or leafy

spurge stem density as the response variables. Small ruminant grazing and herbaceous biomass were included as fixed effects and transect identity and year were included as random variables. Amongst the models testing for associations between leafy spurge and different functional groups, we excluded exotic forbs as exotic forbs other than leafy spurge were only present in 15% of plots, whereas all other functional groups were present in at least 50% of plots. Native forb and exotic grass relative abundances were square-root transformed to normalise the residuals. When testing for leafy spurge associations with forage production data, we used linear models with either graminoid biomass or graminoid nitrogen content (as a proxy for quality) as response variables because forage production data were collected at the transect level. Graminoid biomass was square-root transformed to normalise the residuals.

The models for the multi-site survey were similar to those used for the single-site survey. For these models, however, we included two management variables (past usage [cattle or recreation] and leafy spurge management [herbicide or other] and three additional covariates because more environmental data were collected. The covariates included: herbaceous biomass (square-root transformed to reduce the influence of outliers), soil sand content, soil carbon and soil phosphorus. Soil silt, clay and nitrogen were collected, but not included as they were highly collinear with the selected covariates. To test whether management or the environment affected leafy spurge abundance, we used a mixed model with leafy spurge cover as the response variable and the environmental and management variables as predictors. The random structure included the block nested within a region and the year of sampling. We initially included site as a random factor in all analyses from the multi-site survey to account for multiple blocks within a single site, but removed it from our final analysis because only some regions had multiple sites and only some sites had multiple blocks. Additionally, its inclusion in the model typically increased the AIC score. Most models testing for leafy spurge associations with the plant community were similarly structured as above, but included leafy spurge cover and its interactions with past usage and management as fixed effects. Interaction terms were removed if they increased AIC scores. The response variables were the same as the single-site survey, except we did not analyse shrub richness or abundance as shrubs were only present in 28% of plots. Unlike the single-site survey, the forage models were analysed as mixed models. Forage production and nitrogen content were analysed as other multi-site models; however, phosphorus content was only measured in 2019, so year of sampling and block identity were not included as random effects because there was no repeated sampling.

Results

Trait differences amongst plant functional groups

Average height ($F_{4,88} = 10.96$, $P < 0.001$), SLA ($F_{4,76} = 3.00$, $P = 0.024$) and root diameter ($F_{4,78} = 3.27$, $P = 0.016$) differed amongst the functional groups, whereas leaf area ($F_{4,75} = 1.35$, $P = 0.258$) and SRL ($F_{4,77} = 1.04$, $P = 0.391$) did not (Fig. 1). Shrubs were

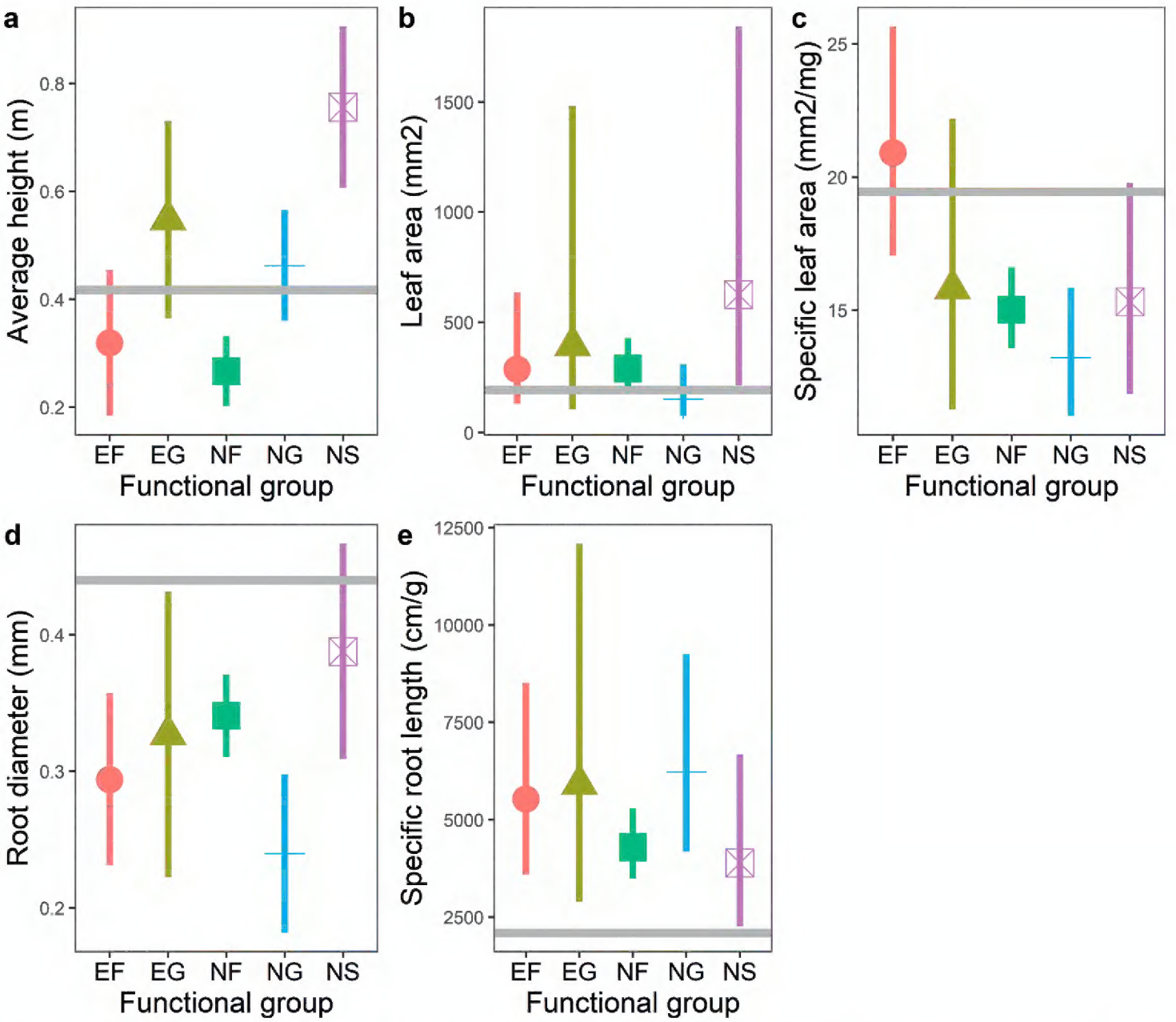

Figure 1. Differences in height (**a**), leaf area (**b**), specific leaf area (**c**), root diameter (**d**) and specific root length (**e**) amongst the functional groups considered in this study. Functional groups are abbreviated as follows: EF – exotic forb, EG – exotic graminoid, NF – native forb, NG – native graminoid, NS – native shrub. Points represent means and lines 95% confidence intervals. Solid grey horizontal lines denote the mean trait values for leafy spurge (*Euphorbia esula*).

tallest, with graminoids intermediate and forbs shortest, regardless of origin (Fig. 1a). Exotic forbs had greater SLA than all other functional groups, which did not differ from each other (Fig. 1c). Native shrubs also had the thickest roots, while native graminoids had the thinnest and other functional groups were intermediate (Fig. 1d).

Leafy spurge associations with management and the environment

We found no significant relationships between leafy spurge relative cover and small-ruminant grazing or productivity in the single-site survey or between leafy spurge cover and any management or environmental variables in the multi-site survey (Table 1), suggesting that leafy spurge relative abundance is relatively independent of the measured covariates. We did find a positive relationship between leafy spurge absolute

Table 1. Mixed model results testing for the relationship between leafy spurge abundance and management or environmental covariates in the single-site and multi-site surveys.

Survey	Response	Factor	Estimate	SE	df	t	P
Single-site	Cover	Grazing	0.011	0.042	27.8	0.27	0.790
		Productivity	0.012	0.007	27.8	1.63	0.115
	Density	Grazing	1.228	1.492	25.9	0.82	0.418
		Productivity	0.589	0.264	25.9	2.23	0.035
Multi-site	Cover	Grazing	-0.068	0.041	68.5	-1.62	0.111
		Herbicide	0.039	0.042	26.0	0.94	0.356
		Productivity	0.007	0.007	100.5	1.02	0.309
		Soil C	-0.028	0.032	12.9	-0.87	0.402
		Soil P	-0.002	0.074	61.7	-0.03	0.980
		Soil sand	-0.002	0.002	89.5	-0.93	0.362

abundance, measured as stem density and productivity in the single-site survey, indicating that leafy spurge does become more abundant in more productive sites. Stem density was unrelated to small ruminant grazing, however (Table 1).

Species richness and ecosystem function

Leafy spurge was negatively associated with plant species richness in the intensive single site survey ($F_{2,450}$ = 28.14, P < 0.001; Fig. 2a) and the multi-site survey ($F_{2,194}$ = 3.63, P = 0.028; Fig. 2b). For the multi-site survey, the negative leafy spurge-species richness relationship was consistent across management actions despite greater richness in sites grazed by cattle ($F_{1,20}$ = 5.79, P = 0.026; Fig. 2b). The only other significant predictor of plant species richness was soil phosphorus, where richness declined with phosphorus concentrations (see Suppl. material 1: fig. S1, table S5). Leafy spurge was also associated with a loss of ecosystem function as graminoid forage production declined with leafy spurge abundance in both the single ($F_{2,25}$ = 3.84, P = 0.035; Fig. 2c) and multi-site surveys ($F_{1,42}$ = 7.55, P = 0.009; Fig. 2d). Otherwise, graminoid biomass unsurprisingly increased with overall productivity in both the single-site and multi-site surveys (see Suppl. material 1: tables S4, S5, fig. S2). Interestingly, graminoid phosphorus content increased marginally with leafy spurge abundances ($F_{1,20}$ = 3.84, P = 0.064; Fig. 2e) in the multi-site survey, whereas graminoid nitrogen was not associated with leafy spurge abundance in either survey (see Suppl. material 1: tables S4, S5).

Functional groups

In both the single ($F_{2,442}$ = 6.07, P = 0.003; Fig. 3a) and multi-site surveys ($F_{2,199}$ = 6.78, P = 0.001; Fig. 3e), exotic graminoids became proportionally more abundant as leafy spurge increased. Increases in leafy spurge and exotic graminoids corresponded with a loss of native forbs ($F_{2,445}$ = 8.88, P < 0.001; Fig. 3c) and shrubs ($F_{1,400}$ = 4.68, P = 0.031; Fig. 3d) in the single-site survey, while native graminoid abundance was

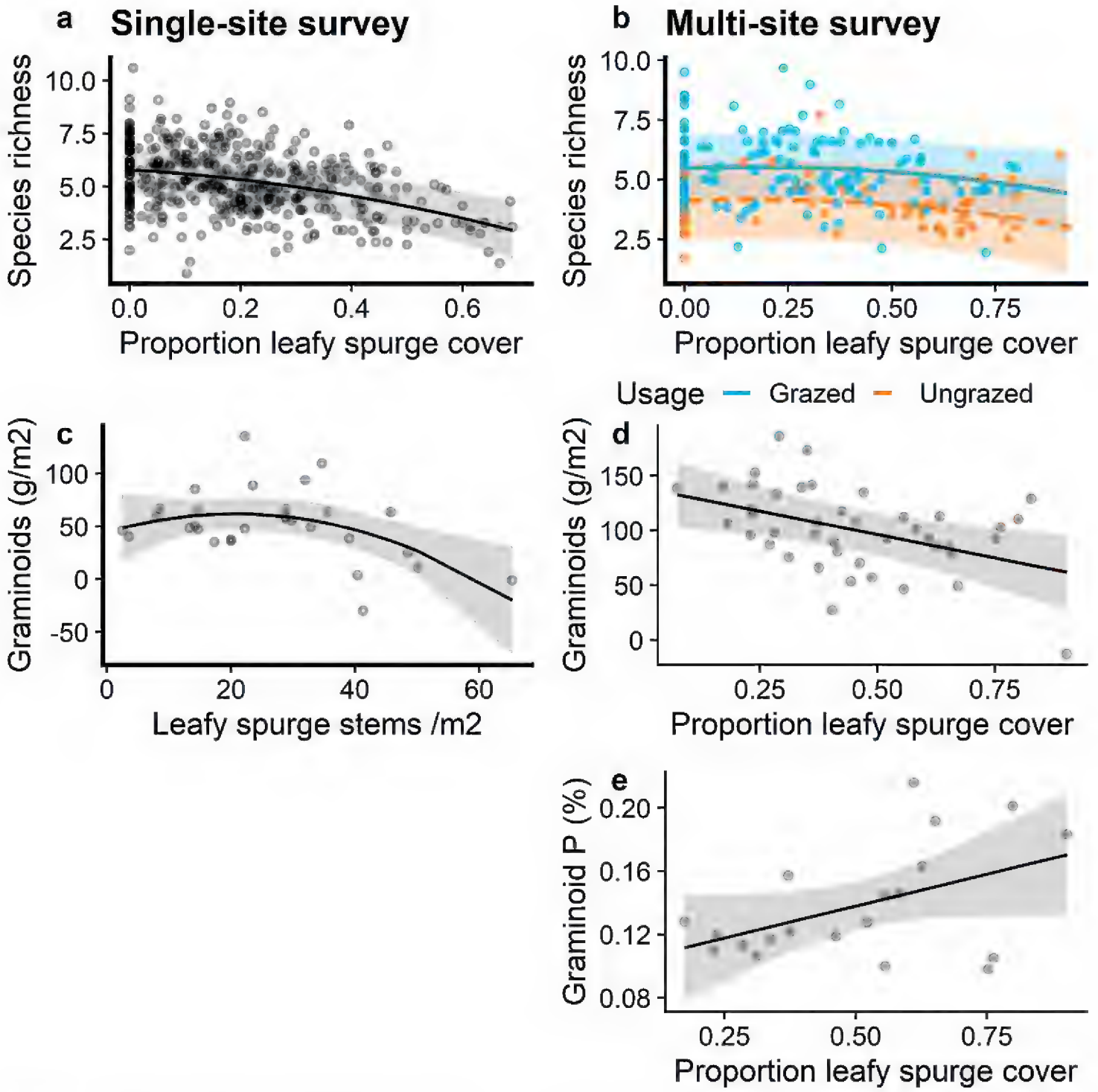

Figure 2. The relationship between leafy spurge cover, plant species richness and forage production. The relationship between leafy spurge and total species richness are shown for the intensive local survey (**a**) and the multi-site survey (**b**). Forage production was assessed for graminoid biomass for the single (**c**) and multi-site (**d**) surveys and as graminoid phosphorus content, but only for the multi-site survey. Management actions are colour-coded as per figure legends. There were no significant relationships between leafy spurge abundance and graminoid nitrogen content in either survey (not shown). Leafy spurge abundance was typically assessed as proportional cover, except leafy spurge stem density was a better predictor of graminoid biomass in the single-site survey (**c**). Plots are partial residual plots and fitted lines show the results of quadratic (**a–c**) or linear (**d–e**) regressions with 95% confidence intervals.

unaffected ($F_{1,450}$ = 2.15, P = 0.143; Fig. 3b). Interestingly, the proportion of species that were native graminoids increased at high leafy spurge abundances, but only if the transect was grazed by small ruminants (Fig. 4a). We found no direct relationships between functional group abundances and either small ruminant grazing or

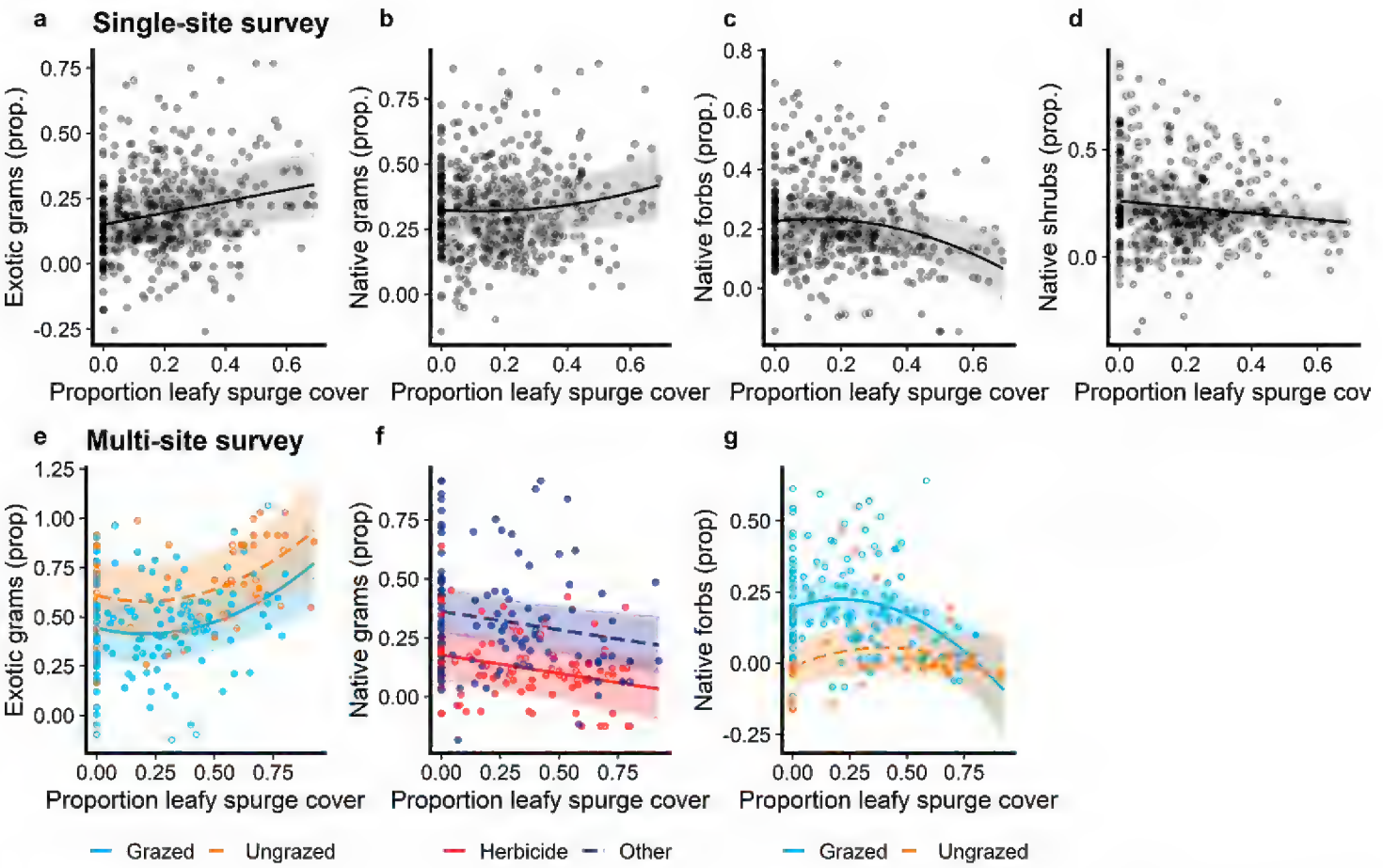

Figure 3. The relationship between leafy spurge cover and the relative abundance of different functional groups in the single (**a–d**) and multi-site (**e–g**) surveys. Shown are the relationship with the proportional cover of exotic graminoids (**a, e**), native graminoids (**b, f**), native forbs (**c, g**) and native shrubs (**d**). Native shrubs were too rare in the multi-site survey to analyse. For the multi-site survey, points and lines are colour-coded by whether the site was grazed by cattle or treated with herbicide to control leafy spurge as shown in the legend. Plots are partial residual plots and fitted lines show the fitted linear (**a, b, d, f**) or quadratic (**c, e, g**) regressions with 95% confidence intervals. All relationships, except for native forbs in the single-site survey, were significant at $P < 0.05$.

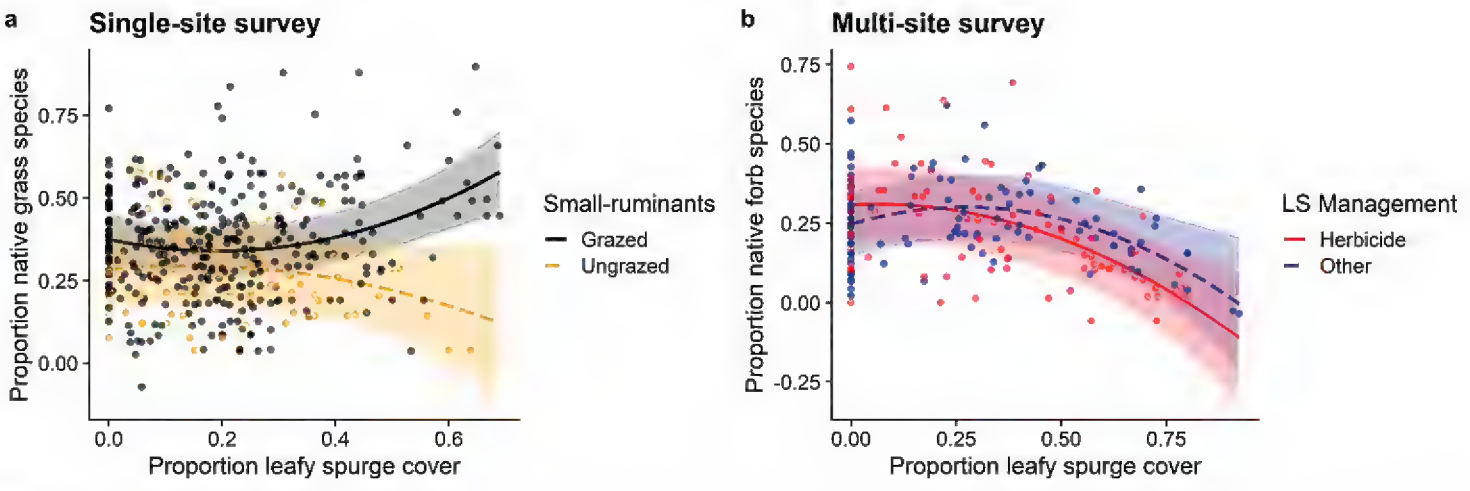

Figure 4. The relationship between leafy spurge cover and the proportion of species classified as native graminoids (**a**) and forbs (**b**). Leafy spurge effects on native graminoid relative richness are shown from the single-site survey, colour-coded as a function of small ruminant grazing. Leafy spurge effects on native forb richness are shown from the multi-site survey and colour-coded as a function of whether herbicide is currently used to manage leafy spurge. Plots show partial residuals. Lines represent best fit lines and shaded areas the 95% confidence intervals around those fits.

Table 2. Summary statistics comparing the single-site and multi-site surveys.

		Single-site survey				Multi-site survey			
Response variable		**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Leafy spurge		0.20	0.16	0.00	0.95	0.27	0.27	0.00	0.92
Diversity									
Species richness		5.0	2.0	1.0	12.0	4.2	2.2	1.0	12.0
Site productivity									
Herb. mass (g/m^2)		112	51	35	268	183	97	50	532
Forage graminoids	Mass (g/m^2)	50	34	8	156	94	80	13	374
	N (%)	1.5	0.2	0.8	2.2	1.2	0.2	0.8	1.8
	P (%)					0.14	0.04	0.09	0.21
Functional groups proportions									
Exotic graminoids	Richness	0.19	0.18	0.00	1.00	0.40	0.30	0.00	1.00
	Cover	0.22	0.24	0.00	1.00	0.51	0.31	0.00	1.00
Native graminoids	Richness	0.34	0.21	0.00	1.00	0.27	0.25	0.00	1.00
	Cover	0.32	0.25	0.00	1.00	0.23	0.27	0.00	1.00
Native forbs	Richness	0.24	0.18	0.00	0.83	0.18	0.21	0.00	0.80
	Cover	0.20	0.21	0.00	0.88	0.16	0.20	0.00	0.78
Native shrubs	Richness	0.17	0.17	0.00	0.75	0.07	0.13	0.00	0.67
	Cover	0.22	0.26	0.00	0.98	0.07	0.14	0.00	0.63
Exotic forbs	Richness	0.03	0.09	0.00	1.00	0.03	0.10	0.00	0.67
	Cover	0.02	0.07	0.00	1.00	0.02	0.09	0.00	0.63
Community weighted trait means									
Height (m)		0.40	0.11	0.21	0.78	0.36	0.13	0.21	0.95
Leaf area (cm^2)		5.46	0.52	1.85	6.57	5.55	0.59	4.24	6.94
SLA log(cm^2/g)		2.52	0.15	1.80	2.99	2.61	0.08	2.34	2.86
Root diam (mm)		0.33	0.05	0.18	0.59	0.27	0.08	0.16	0.48
SRL log(cm/g)		8.34	0.45	7.32	9.28	8.85	0.43	7.51	9.46

productivity. In contrast to the single-site survey, native graminoids declined ($F_{1,202}$ = 7.41, P = 0.007; Fig. 3f) and native forbs only declined in grazed systems (interaction $F_{2,206}$ = 3.81, P = 0.024; Fig. 3g) in the multi-site survey, likely because these systems generally had greater forb cover (Table 2). Grazed sites also had less exotic graminoid cover ($F_{1,22}$ = 6.53, P = 0.018), independent of leafy spurge (Fig. 3e). Unexpectedly, sites where leafy spurge is primarily managed through broadleaf specific herbicide had less native grass ($F_{1,22}$ = 21.97, P < 0.001), while forbs cover was unaffected ($F_{1,14}$ = 0.01, P = 0.944). Native forb richness did decline, however, in herbicide-treated sites when leafy spurge cover was high (interaction $F_{2,202}$ = 4.91, P = 0.008; Fig. 4b). Otherwise, the relationship between leafy spurge abundance and the richness of each functional group was similar to the relationships found for proportional cover (see Suppl. material 1: tables S6, S7). In addition to the relationships between functional group abundances and leafy spurge, we found that soil carbon and soil phosphorus affected the relative abundances of the functional groups. Native graminoids increased and native forbs declined with increasing soil carbon, whereas exotic graminoids decreased with productivity and increased with soil phosphorus (see Suppl. material 1: fig. S3, table S7), indicating that the measured environmental covariates were important for community assembly despite having no effect on the abundance of leafy spurge.

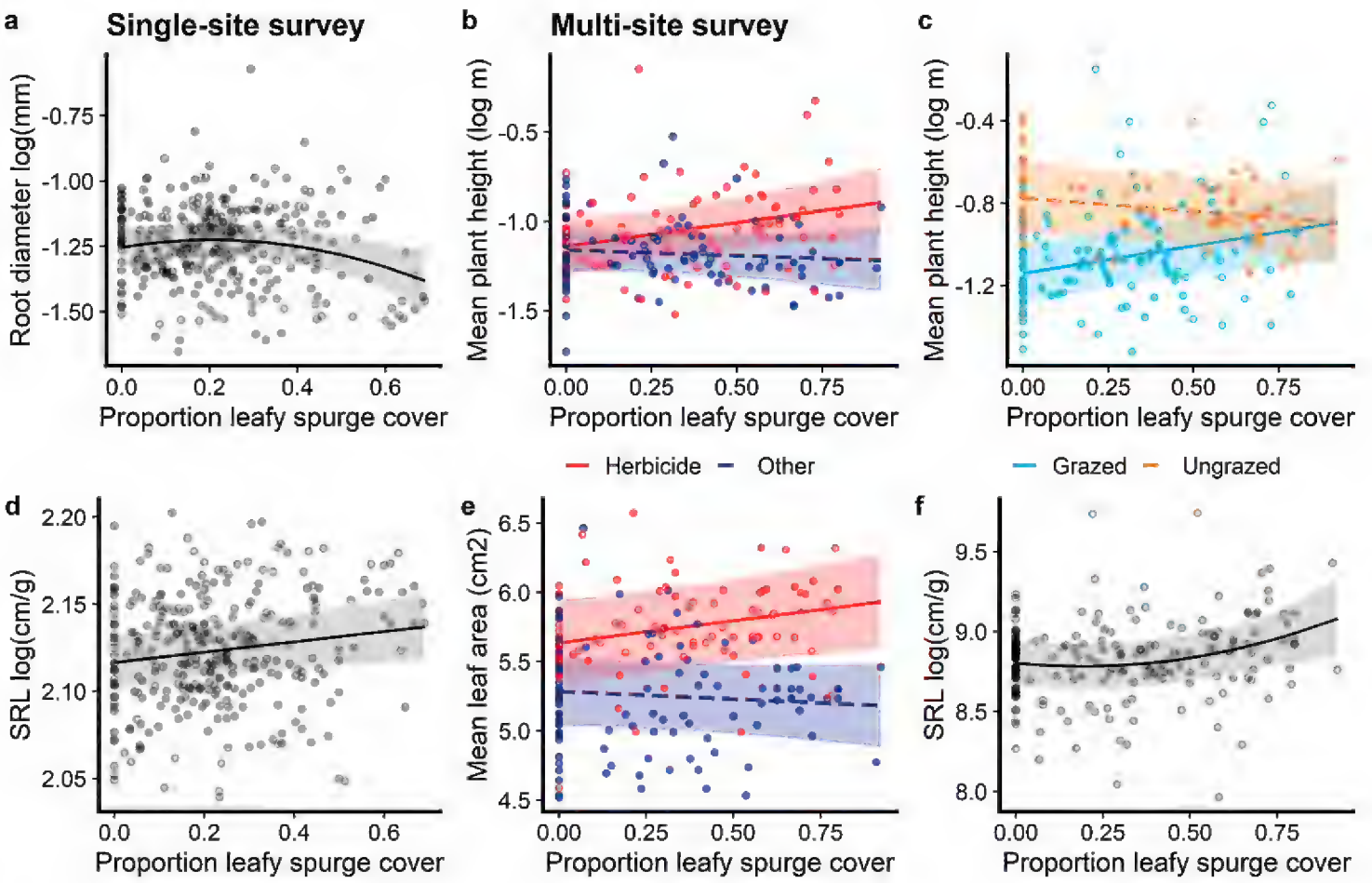

Figure 5. Significant relationships (P < 0.05) between leafy spurge cover and community weighted trait means in the single-site (**a, d**) and multi-site surveys (**b, c, e, f**). In the single-site survey, root diameter declined (**a**) and specific root length (SRL) increased (**d**) with leafy spurge abundance. In the multi-site survey, the relationship between leafy spurge cover and average height was dependent on both the leafy spurge management strategy (**b**) and whether the site was grazed (**c**), whereas the relationship with leaf area was dependent only on management strategy (e) and the relationship with specific root length (SRL) was independent of other factors (**f**). Management and grazing are colour-coded as in the legends. All plots are partial residual plots. Lines represent best fit lines and shaded areas the 95% confidence intervals around those fits.

Community-weighted trait means

Leafy spurge cover was negatively associated with community-weighted mean root diameter ($F_{2,313} = 3.45$, $P = 0.033$; Fig. 5a) and positively associated with SRL ($F_{1,308} = 4.58$, $P = 0.033$; Fig. 5d) in the single-site survey, although root diameter only declined at higher leafy spurge abundances. Otherwise, no traits were significantly associated with leafy spurge abundance (see Suppl. material 1: table S8). In the multi-site survey, SRL also increased at higher leafy spurge abundances ($F_{2,182} = 3.76$, $P = 0.025$; Fig. 5f). The relationship between leafy spurge abundance and plant height was more complex. Plant height increased with leafy spurge abundances in herbicide-treated (Fig. 5b) and grazed systems (Fig. 5c), whereas it was not significantly associated with leafy spurge abundance otherwise (spurge by management interaction $F_{1,185} = 7.56$, $P = 0.007$; spurge by grazing interaction $F_{1,182} = 10.94$, $P = 0.001$). The relationship between mean leaf area and leafy spurge cover also depended on leafy spurge management, increasing in herbicide-treated systems, but unrelated in others (spurge by management interaction $F_{1,182} = 4.45$, $P = 0.036$; Fig. 5e). Neither SLA nor root diameter were associated

with leafy spurge abundances in the multi-site survey (see Suppl. material 1: table S9). We found no significant relationships between any of the other covariates and any community-weighted means in either survey (see Suppl. material 1: tables S8, S9).

Discussion

The relationships between leafy spurge abundance and plant species richness and forage production were relatively consistent. As these relationships were found in multiple surveys and after accounting for management differences and underlying environmental relationships, this suggests that leafy spurge invasion drives the loss of species and ecosystem function. Some unmeasured factor may still drive ecosystem degradation and leafy spurge invasion occurs as a result, as invasive grasses positively covaried with leafy spurge, although we lack such evidence. Amongst the traits measured, only community SRL consistently covaried with leafy spurge abundance, indicating some role of belowground interactions during leafy spurge invasion. All other functional groups and trait relationships with leafy spurge abundance either differed between the two surveys (declines in native graminoids, changes in root diameter) or depended on site management (loss of native forbs, changes in plant height and leaf area). Combined, these results suggest that broader impacts of invasion, like the loss of species and changes in ecosystem function, may be relatively consistent amongst locations. Any effects on plant community functional structure largely depend on both the scale of the investigation, as well as the management history of the locations included, suggesting that deciphering leafy spurge effects on community traits may be challenging using only surveys.

Consistent impacts of leafy spurge

Declines in plant diversity and ecosystem function are a commonly observed consequence of invasion, both in general (Vilà et al. 2011) and for leafy spurge specifically (Belcher and Wilson 1989; Butler and Cogan 2004; Larson and Larson 2010). We found consistent negative relationships between leafy spurge abundance and both species richness and forage production, consistent with these findings. Whether the declines in richness and forage production are linked is unclear. Declining biodiversity due to invasion can lead to declines in ecosystem function (Linders et al. 2019), which may help explain the declines in forage production. In the current study, it is more likely that leafy spurge dominance reduces graminoid productivity because productivity is typically resource limited in grassland ecosystems (Stevens et al. 2015). Interestingly, the phosphorus content of the forage produced increased marginally alongside leafy spurge abundance. As leafy spurge abundance was unrelated to soil phosphorus, this suggests some change in how the graminoids access nutrients. Leafy spurge invasion can increase the abundance and diversity of mycorrhizal fungi (Lekberg et al. 2013), which can transfer large amounts of phosphorus to their host plants (Delavaux

et al. 2017). If the remaining graminoids can exploit the mycorrhizal fungi, this would explain the increase in phosphorus content. Nonetheless, increased phosphorus appears insufficient to allow the graminoids to competitively suppress leafy spurge.

Despite declines in overall graminoid biomass, exotic graminoids were consistently composed of a greater portion of the resident community at high leafy spurge abundances. Similar positive associations between leafy spurge and exotic grasses have been reported elsewhere (Belcher and Wilson 1989; Larson and Larson 2010). Exotic species can aggregate in invaded areas (Stotz et al. 2020). Positive associations amongst exotic species may be because exotic species can better tolerate competition (Golivets et al. 2018), because they facilitate each other (i.e. invasional meltdown; Simberloff and Von Holle (1999)) or because degraded systems allow for increased invasion (more passengers) regardless of species identity (MacDougall and Turkington 2005). Each of the main exotic grasses in our study (*Poa pratensis*, *Bromus inermis*, *Agropyron cristatum*) can reduce plant diversity when they invade and are considered strong competitors (Henderson and Naeth 2005; Bennett et al. 2014; Toledo et al. 2014). Being able to compete with leafy spurge is not likely to drive the positive leafy spurge-invasive grass association, however, as native and exotic grasses can compete similarly with leafy spurge (Rinella and Sheley 2005) and native grasses are not positively associated with leafy spurge. We cannot rule out facilitation between leafy spurge and invasive grasses as all of these species can cause diversity declines, which could reduce biotic resistance and facilitate later arriving invaders (Byun et al. 2018). Both leafy spurge and the grasses could also invade grasslands degraded for unrelated reasons (Chabrerie et al. 2008; White et al. 2012), but we found no evidence that current management affects positive relationships amongst invasive species, suggesting that a purely passenger model is unlikely. We lack information on the intensity and frequency of those management actions or historical management in these systems. Overgrazing or overuse of herbicides, either currently or in the past, could cause ecosystem degradation leading to greater invasion (DiTomaso 2000; Lekberg et al. 2017), so we cannot completely rule out the passenger model. More directed experiments would be required to differentiate amongst these mechanisms.

Leafy spurge invasion was also consistently associated with high SRL in the neighbouring plants, which is associated with acquisitive belowground strategies (Freschet et al. 2018; Bergmann et al. 2020). High SRL in species co-existing with leafy spurge suggests that these species need to be effective in taking up soil resources. As we found no relationships between any of the measured soil variables and leafy spurge abundance, we hypothesise that species with high SRL are more effective in competing with leafy spurge rather than having both SRL and leafy spurge abundance covary along an environmental gradient. As SRL and root diameter are typically negatively correlated (Bergmann et al. 2020), this may be why root diameter declined in the single-site survey, although it is unclear why a similar relationship was not found in the multi-site survey. An increase in acquisitive root traits also suggests that limiting similarity (MacArthur and Levins 1967) drives co-existence during leafy spurge invasion, as leafy spurge typically has thicker fine roots with lower SRL than the resident species (Fig. 1).

Conversely, leafy spurge induced increases in mycorrhizal fungi (Lekberg et al. 2013) likely do not benefit other thicker-rooted species to the extent that allows co-existence.

The positive relationship between acquisitive root traits and co-existence with leafy spurge are likely partially independent of the changes in functional group composition. Exotic graminoids increased with leafy spurge abundance, but varied greatly in root diameter and SRL. Native graminoids had the thinnest roots of any functional group, but declined with leafy spurge abundance in the multi-site survey and were largely unrelated to leafy spurge in the single-site survey. Interestingly, native graminoid richness increased with leafy spurge abundance when leafy spurge was grazed by small ruminants, but declined in the absence of leafy spurge control. Grazing can reduce the competitive ability of most species, including leafy spurge (Rinella and Bellows 2016), by reducing light interception capability and reducing resource allocation to root systems (May et al. 2009). Reductions in above- and belowground competition may be sufficient for native graminoids with acquisitive root traits, which are typically more competitive with thicker-rooted species like leafy spurge (Bennett et al. 2016), to persist when leafy spurge is otherwise dominant. Nonetheless, native graminoids do not comprise a large proportion of cover, potentially due to displacement by invasive grasses (Bennett et al. 2014). More abundant invasive grasses (Table 2) may also explain the lack of persistence of native graminoids in the multi-site survey.

Land management and leafy spurge effects on community structure

Despite some consistency amongst land uses and control strategies, the observed relationships between leafy spurge and the plant community also changed with land management. Invasion and land management both have well documented and, sometimes, divergent effects, on plant communities (Diaz et al. 2007; Saar et al. 2017; Hejda et al. 2019; Sodhi et al. 2019). When multiple processes act upon community assembly, the signal of any one process can be lost (Spasojevic and Suding 2012; Bennett and Pärtel 2017). As each of the land management actions altered community structure and the observed relationship between leafy spurge abundance and the functional composition of the community, this suggests that the management regime may affect conclusions drawn about how leafy spurge affects the plant community. Whether these differing conclusions actually reflect context-specific impacts of leafy spurge or if both leafy spurge and the plant community are responding to the same set of cues would likely vary case by case.

Cattle grazing was the factor most associated with differences in the relationship between leafy spurge and the plant community, suggesting that failing to consider grazing may result in erroneous conclusions. Grazed sites had more species and a greater abundance and diversity of forbs than ungrazed sites, consistent with models and data showing that moderate cattle grazing increases species richness and forb abundances by limiting graminoid dominance (Milchunas et al. 1988). Interestingly, we also found less invasive grass in cattle-grazed pastures than ungrazed pastures. As invasive grasses are a major cause of biodiversity loss in the northern Great Plains (DiTomaso 2000), grazing of the invasive grasses by cattle may help conserve plant biodiversity, as has

been shown in some targeted grazing studies (Rhodes et al. 2021). As many forbs were absent from ungrazed sites even at low leafy spurge abundances, we detected no relationship in these sites, suggesting that most of the forb loss in invaded pastures may be caused by invasive grasses which were more abundant when ungrazed. The lack of forbs across ungrazed sites and heavily invaded patches suggests that both leafy spurge and invasive grasses can cause the loss of forbs from invaded communities. Other management actions may still drive the abundances of both invasive species and forbs. Without further information on how invasive and native populations change over time or experimental manipulation of management regimes (Sokol et al. 2017; Kulmatiski and Beard 2019), it will not be possible to differentiate amongst these mechanisms.

We hypothesised that plant traits would help clarify how cattle grazing mediates the relationship between leafy spurge and the plant community, but many of these relationships were inconsistent, especially when considering plant height. In the multi-site survey, plant height increased with leafy spurge abundance in grazed sites, but decreased with leafy spurge in ungrazed sites, whereas, in the intensive survey, we found no relationship between plant height and leafy spurge abundance. There are many mechanisms that could account for these patterns. A positive relationship between leafy spurge abundance and plant height could represent competitive exclusion of shorter species (Hejda et al. 2019) or it could result from associational defences (Callaway 1995) where avoidance of leafy spurge patches by cattle (Kronberg 1993) reduces grazing on taller plants (Diaz et al. 2007). The intensively studied site, however, was less productive, which could limit any inference about invasion impacts if the range of conditions surveyed were too narrow (Pyšek et al. 2012). The intensive site also had more tall shrubs, which were negatively related to leafy spurge abundance. Exclusion of leafy spurge from shrub-dominated areas would also result in taller plants at low leafy spurge densities. By contrast, the loss of short forbs in ungrazed sites due to competition with tall invasive grasses (Cadotte 2017) may result in the plant community being taller when leafy spurge is at low densities. While they remain conjecture, each of these hypotheses can be tested by manipulating grazing at sites differing in both productivity and leafy spurge abundance and monitoring shifts in the plant community.

As with cattle grazing, herbicide use was associated with multiple changes in the plant community. Broadleaf specific herbicides are usually used for leafy spurge control and typically result in forb losses and increased grass growth (Lym and Messersmith 1985; Thilmony and Lym 2017). Surprisingly, native graminoids were much less abundant in herbicide treated sites, whereas the diversity of native forbs declined, but only at high leafy spurge abundances. Herbicide usage can result in secondary invasions that can have detrimental effects on native species (Pearson et al. 2016); however, we found no evidence that herbicide increased other invaders, leaving the mechanism for native grass loss unclear. Herbicide resistance may allow some forb species to increase following herbicide application (Thilmony and Lym 2017), which could account for the lack of a difference in forb abundance between treated and untreated sites. That forb richness declined at higher leafy spurge densities could result from the combined effects of herbicide and competition (Adcock and Banks 1991) or cumulative herbicide injury if herbicides were more frequently applied in more invaded areas (Simmons et al.

2007). Plant communities at herbicide-treated sites also increased in height and leaf area as leafy spurge abundance increased. Frequent herbicide use may increase nutrient flushes as plants die, increasing the resources available to unaffected species (Gaupp-Berghausen et al. 2015), which could increase the abundance of faster growing species which tend to be taller with larger leaves (Reich 2014). Current herbicide usage may also be correlated with other unmeasured management factors which may bias our interpretation of the results; however, we lack the data to make any such conclusions.

Conclusions

Although the mechanisms may be unclear, management differences amongst sites undoubtedly can alter conclusions drawn when using survey-based approaches to infer the effects of invasive species. That some relationships were consistent across different management regimes suggests that some effects of invasive species, such as losses of diversity and ecosystem function and association with other invasive species, are likely characteristic of leafy spurge invasion and strong enough to overcome any noise due to differences amongst sites. By accounting for different management regimes, however, we can develop hypotheses about scenarios under which leafy spurge may be the driver or passenger of community change. These hypotheses can then be tested by manipulating management activities along environmental and leafy spurge invasion gradients to improve our understanding of the causes and consequences of leafy spurge invasion.

Acknowledgements

We would like to thank Jacqueline Gelineau, Christopher Thorpe, Anna Jacobson and Amanda Mitchell for their help with collecting plant community data and processing samples. This research was supported by funding to JAB from an NSERC Discovery Grant, an NSERC Collaborative Research and Development Grant, the Saskatchewan Cattlemen's Association and the University of Saskatchewan and from funding to JFC from the University of Alberta Rangeland Research Institute and an NSERC Discovery Grant. CL was supported by an NSERC USRA and TG by a University of Saskatchewan USRA.

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Supplementary material 1

Supplemental information and results from Groff Liu et al. Management efffects on leafy spurge invasion impacts

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Data type: tables and figures

Explanation note: Approximate location of each site used in the multi-site survey. The number of trait values extracted from each of the sources. AIC scores for models testing whether leafy spurge cover or leafy spurge density was a better predictor of the various response variables in the single-site model. Model results showing the relationship among leafy spurge abundance, species richness and forage production in the single-site survey. Model results showing the relationship among leafy spurge abundance, species richness and forage production in the multi-site survey. Plant species richness as a function of soil phosphorus. Graminoid productivity as a function of site productivity in the single site (A) and multi-site (B) surveys. ANOVA tables showing leafy spurge abundance effects on the proportional richness and abundance of different functional groups in the intensive single site survey. ANOVA tables showing leafy spurge abundance effects on the proportional richness and abundance of different functional groups in the intensive single site survey. Environmental covariate relationships with functional group relative abundances. Leafy spurge effects on community weighted means and functional dispersion of height, leaf area, specific leaf area (SLA), root diameter and specific root length (SRL) in the intensive single site survey.

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Link: https://doi.org/10.3897/neobiota.81.89450.suppl1